

New species and records of pseudothelphusid crabs (Crustacea: Brachyura) from Central America in the Museum of Natural History of Tulane University

Gilberto Rodríguez

Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 21827,
Caracas 1020 A, Venezuela, email grodrigu@oikos.ivic.ve;

Abstract.—Two new species of freshwater crabs are described. *Potamocarcinus vulcanensis*, new species, from El Salvador, resembles *P. zilchi* (Bott, 1956) in the sickle-shaped appearance of its first gonopods, but lacks the elongated and spinulous cephalic process of this species. *Ptychophallus osaensis*, new species, from Costa Rica, is characterized within the genus by the long geniculated apex and the small knob-like lobe of the lateral expansion of the first gonopods. *Phrygiopilus ibarra* (Pretzmann, 1980) is redescribed and new records for six other species of Pseudothelphusidae are also given.

The somatic morphology of the Pseudothelphusidae offers few reliable characters for the discrimination of the different taxa. In most cases, it is only possible to establish generic and specific differences by the examination of the first male gonopods. Failure to recognize this fact made the systematics of these Neotropical freshwater crabs extremely complex (Schmitt 1969), until the standardization of the nomenclature for the description of this appendage by Smalley (1964a) who then subdivided the old genus *Pseudothelphusa* Saussure, 1857, into more rational taxonomic units (Rodríguez & Fitzpatrick 1996). Most of the material used to accomplish this task (Smalley 1964a) came from his field trips to Costa Rica, Guatemala, Nicaragua and Mexico.

After the decease of this distinguished carcinologist in 1994 (Rodríguez & Fitzpatrick 1996), the rich collection of freshwater crabs deposited by him at the Museum of Natural History of Tulane University was entrusted to the author for curation. Some of the species from Ecuador and Co-

lombia in that collection have already been dealt with in publications by Rodríguez & von Sternberg (1998). The present contribution focusses on several species that were not recorded by Smalley in his Central American papers (Smalley 1964b, 1965, 1970), including two new species.

Abbreviations used are cl. for carapace length and cb. for carapace breadth. The materials recorded are deposited in the Museum of Natural History of Tulane University, New Orleans (TU). Smalley field numbers are abbreviated as AES.

Systematics

Family Pseudothelphusidae Rathbun, 1893
Genus *Potamocarcinus* H. Milne Edwards,
1853

Potamocarcinus aspoekorum (Pretzmann,
1968)

Material.—Belize: Oak Burn Creek, Mountains Pine Ridge, 20 Apr 1973, leg. Ding, 1 young male, cl. 10.4 mm, cb. 15.4 mm (TU 6314); Mollejon Creek, Mountains Pine Ridge, Cayo County, 7 Jul 1973, 1 ju-

venile male, cl. 9.3 mm, cb. 13.5 mm (TU 6329 ex Southern Illinois University Edwardsville Collections); Little Vaqueros Creek, Mountains Pine Ridge, 20 Apr 1973, 1 juvenile female, cl. 9.5 mm, cb. 14.5 mm (TU 6328).

Potamocarcinus magnus (Rathbun, 1896)

Material.—Costa Rica: Tabarcia, San José Province, 16 Feb 1960, leg. R. D. Suttkus & S. Jiménez-Canossa, 1 male juvenile, cl. 9.6 mm, cb. 13.8 mm (TU 4709); Rio Parrita, San José Province, 1 mile NW Tabarcia, tributary of Rio Candelaria, 17 Jul 1962, leg. A. E. Smalley & I. Smalley AES-298, 2 male juveniles, cl. 13.3 and 13.8 mm, cb. 18.9 and 19.6 mm (TU 4452); Rio Grande de Tárcoles, 3 miles E Atenas, small tributary on east bank of Tárcoles, 0.5 miles from Atenas-Alajuela highway, 7 Jul 1962, leg. A. E. Smalley & I. Smalley AES-282, 2 males, cl. 18.2 and 14.6 mm, cb. 27.2 and 21.3 mm, 1 female 21.9 mm, cb. 33.0 mm (TU 4437).

Potamocarcinus richmondi (Rathbun, 1893)

Material.—Costa Rica: 16.3 miles east of Turrialba, walking on road, 28 Jun 1973, leg. R. D. Suttkus & S. Jiménez-Canossa, 1 male, cl. 52.3 mm, cb. 78.7 mm (TU 98-101).

Potamocarcinus vulcanensis, new species
Fig. 1

Material.—El Salvador: Volcán Monte Cristo, 25 km N of Metapán, 2300 m alt., 10 May 1971, leg. S. Peck, 1 male holotype, cl. 12.8 mm, cb. 19.4 mm, 16 male paratypes, the 10 largest cl. 9.8–11.8 mm, cb. 15.2–17.8 mm, 4 ripe female paratypes, cl. 14.8–16.0 mm, cb. 22.8–24.8 mm, 15 immature females (TU 6273).

Type locality.—El Salvador: Volcán Monte Cristo, 25 km N of Metapán, 2300 m alt.

Diagnosis.—First gonopods with margin

forming distally rounded subapical projection bent cephalically, with elongated basal swelling; caudal distal border cup-shaped, applied against cephalic apical border, leaving slit-like aperture between them; strong beak-like mesial process, with stout spine at base on cephalic surface.

Description of holotype.—Carapace 1.50 times as wide as long, surface smooth and polished; cervical grooves shallow, straight, forming wide depression on proximal half, not reaching margins of carapace; anterolateral margins between postorbital angle and level of cervical grooves straight, without postorbital notch, with about 10 depressed papillae; rest of border with flattened or squamiform, closely-set papillae (Fig. 1E). Postfrontal lobes absent, except for two shallow depressions on postfrontal area; middle groove faintly indicated. Surface of carapace between postfrontal lobes and front flat, slightly inclined forward and towards middle line. Upper margin of front in dorsal view slightly bilobed, rounded, ill defined, devoid of conspicuous papillae; lower margin strongly sinuous, advanced in front of upper margin; front low, of unequal height throughout.

Exognath of third maxilliped 0.86 length of ischium of endognath. Palm of largest cheliped (right) moderately swollen, with lower margins sinuous; fingers gaping (Fig. 1D).

First gonopods wide in latero-mesial direction, narrow in caudo-cephalic direction; margin forming distally rounded subapical process bent cephalically, with elongated basal swelling (Fig. 1A); strong beak-like mesial process, with stout spine at base on cephalic surface (Fig. 1B); caudal apical border cup-shaped, deflected cephalically and applied against cephalic apical border to enclose field of spines, leaving slit-like aperture between them (Fig. 1C).

Etymology.—The specific epithet *vulcanensis* alludes to the location of the species on the slopes of the Monte Cristo Volcano.

Remarks.—This species, together with *Potamocarcinus aspoekorum* (Pretzmann, 1968) and *P. zilchi* (Bott, 1956), forms a natural

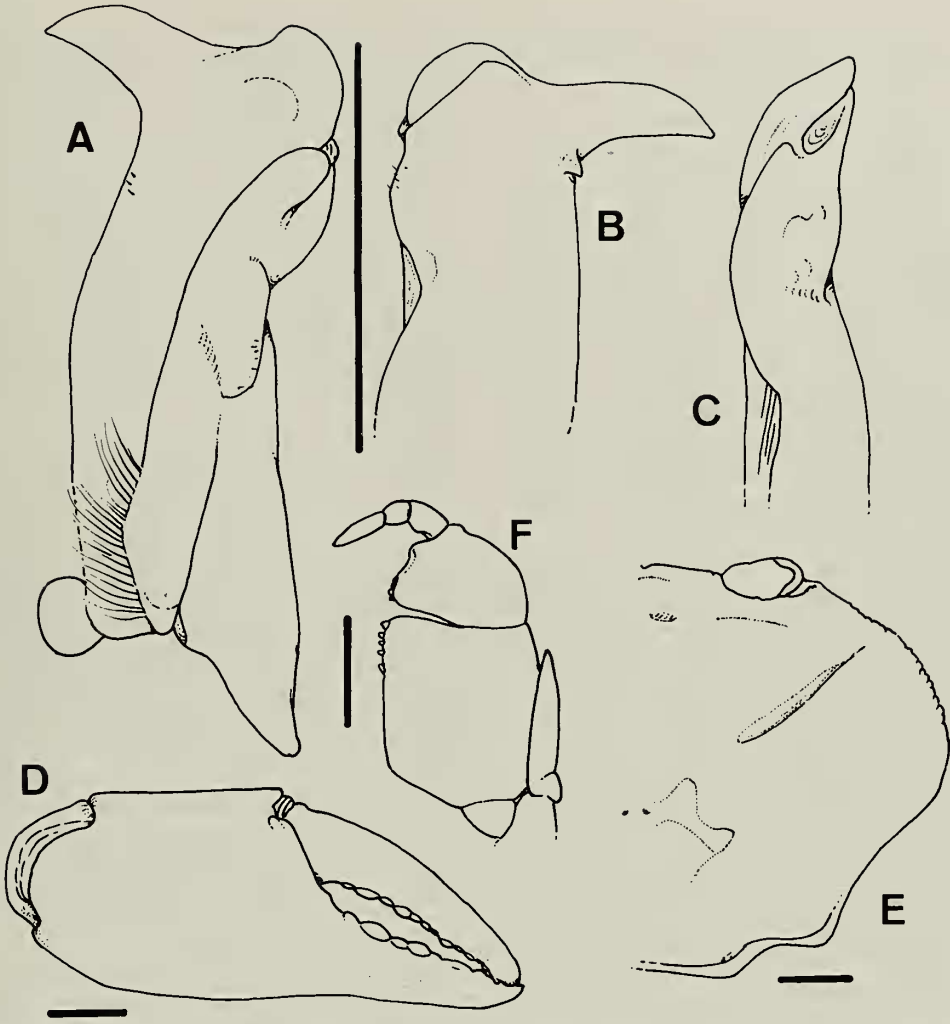


Fig. 1. *Potamocarcinus vulcanensis*, new species, holotype male from Volcán Monte Cristo, 25 km N of Metapán, Santa Ana Department, El Salvador (TU 6273): A–C, first left gonopod; A, caudal; B, apex, cephalic; C, apex, lateral; D, chela of largest cheliped, external view; E, dorsal view of right side of carapace; F, third maxilliped. Scale bars = 2 mm.

group within *Potamocarcinus*, characterized by a first gonopod with a marginal projection (Fig. 1A), a strong mesial process with a spine on the base on the cephalic surface (Fig. 1B), and a caudal apical border bent over the apex (Fig. 1C). Pretzmann (1968) grouped *P. aspeokorum* and *P. zilchi* in the subgenus *Zilchia* Pretzmann, 1968. However, Rodríguez (1982) did not recognize this subgenus because all the characters used to separate *Zilchia* are already present, although not fully developed, in other species of *Potamo-*

carcinus. *Potamocarcinus zilchi* closely resembles the new species in the sickle-shaped appearance of the first gonopods, but can be distinguished by a cephalic process that is strongly elongated and spinulose, covering the field of spines like a lid.

Phrygiopilus Smalley, 1970

Phrygiopilus ibarra (Pretzmann, 1980)

Fig. 2

Material.—Guatemala: km 30 on road from José Pinula to Mataquesquintla, Gua-

temala Department, 10 Aug 1967, leg. A. E. Smalley, AES 406, 3 males, cl. 6.5–9.9 mm, cb. 9.6–14.8 mm, 1 female, cl. 8.9 mm, cb. 14.1 mm (TU 6208).

Diagnosis.—First gonopods wide in latero-mesial direction, flat in caudo-cephalic direction; margin curved strongly laterally, ending in rounded, hollow process; sperm channel opens on cephalic surface; caudal surface produced into very long and flat oval supra-apical process covered with spinules near edges; supra-apical process as long as, and broader than proximal part of gonopod; field of spines concealed between supra-apical process and cephalic border of gonopod; bifid process on mesial side at base of supra-apical process.

Redescription.—Carapace with surface smooth and polished, except for few granules on posterior branchial regions, near margins; cervical grooves shallow, slightly recurved, forming wide depressions proximally, not reaching margins of carapace; anterolateral margins lack postorbital notch, with few small dentiform papillae on distal half, rest of border without defined papillae (Fig. 2F). Postfrontal lobes only indicated by shallow anterior depressions; median groove absent, marked only by shallow depression on upper margin of front. Upper margin of front bilobed in dorsal view, well defined but devoid of conspicuous papillae; lower margin thin, moderately sinuous, advanced in front of upper margin; both frontal margins subparallel; front high, of equal height throughout.

Exognath of third maxilliped 0.85 length of ischium of endognath. Palm of largest cheliped (right) not swollen, with lower margin slightly sinuous, fingers gaping (Fig. 2G).

First gonopods wide in latero-mesial direction, flat in caudo-cephalic direction; margin curves strongly laterally, ends in rounded, hollow process (Fig. 2B, s); sperm channel opens on cephalic surface; caudal surface of gonopod produced into very long and flat oval supra-apical process covered with spinules near edges; supra-apical pro-

cess as long as, and broader than proximal part of gonopod; field of spines concealed between supra-apical process and cephalic border of gonopod (Fig. 2C); bifid process on mesial side at base of supra-apical process.

Remarks.—The species was known only from the male holotype collected 14 km South of Guatemala City, near San José Pinula (Naturhistorische Museum, Vienna, N° 4065). Our specimens come from a locality about 15 km to the west of the type locality.

Phrygiopilus yoshibensis Alvarez & Villalobos, 1998

Material examined.—Mexico: Bacgularugum, stream near city of Simojovel (17°12'N, 92°38'W), District of Simojovel, State of Chiapas, drainage of Río Tlacotalpa, and ultimately, Río Grijalva, leg. R. Pineda-López, 25 May 1981, 1 male, cl. 14.1 mm, cb. 24.2 mm, 1 female, cl. 17.4 mm, cb. 29.0 mm, (TU 6286); 3 km N Tapilula on highway to Pichucalco (17°14'N, 93°00'W), leg. R. Pineda-López, 25 May 1981, 1 male, cb. 23.2 mm, posterior edge of carapace broken, 1 female, cl. 19.0 mm, cb. 25.2 mm (TU 6292).

Remarks.—The present records extend the range of the species 80 km to the west of the type locality.

Phrygiopilus montebelloensis Alvarez & Villalobos, 1998

Material examined.—Mexico: Laguna Tzizcao (16°09'N, 91°40'W), Lagos de Montebello, State of Chiapas, leg. R. Pineda-López, 22 May 1951, 1 male, cl. 13.5 mm, cb. 22.9 mm, 2 females, cl. 10.3 and 10.0 mm, cb. 16.2 and 15.7 mm (TU-6257).

Remarks.—These specimens come from a locality almost identical to the type locality, whose coordinates are given by Alvarez & Villalobos (1998) as 16°09'N, 91°39'W.

The species of *Phrygiopilus* occupy two disjunct areas in Central America: (1) Wa-

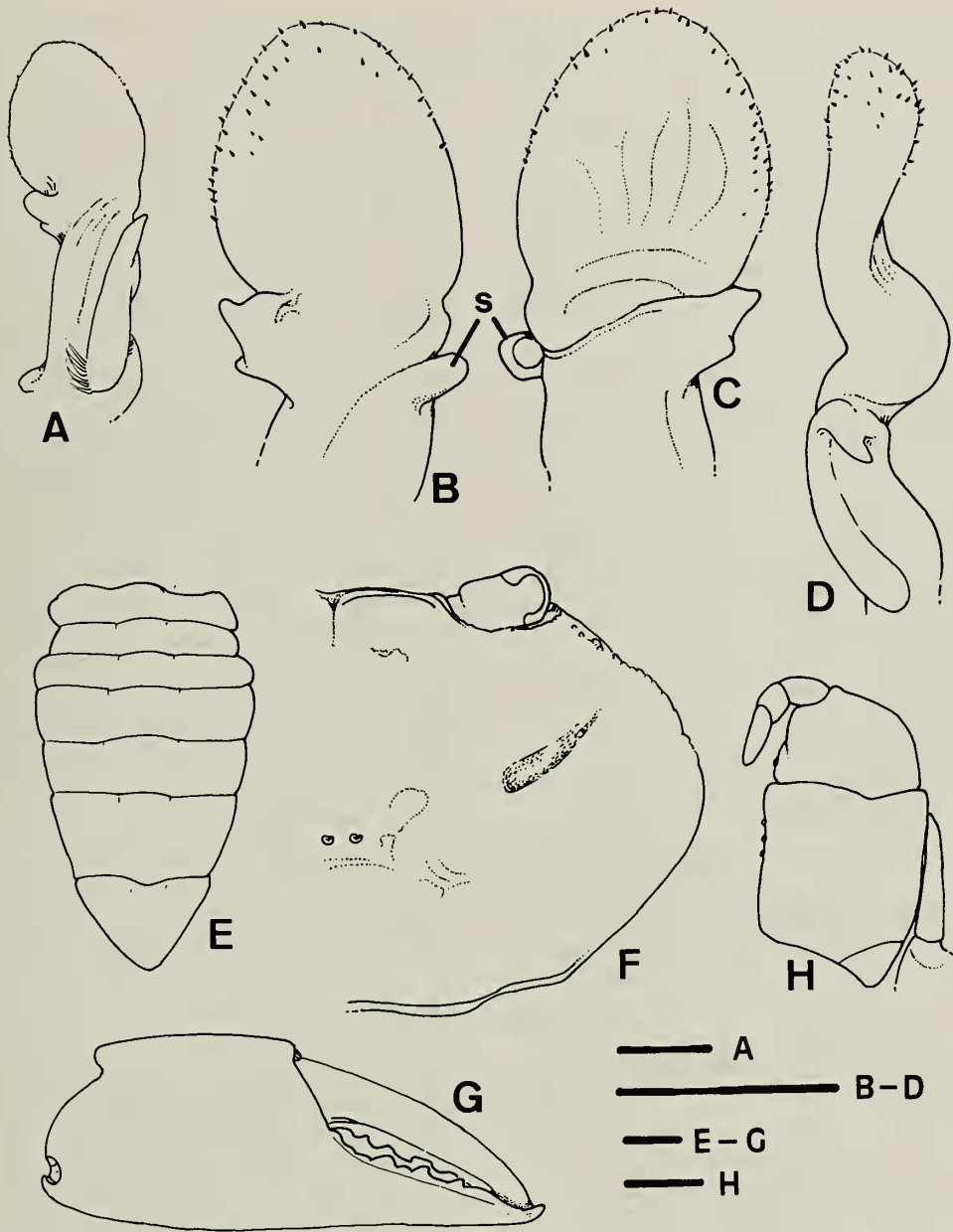


Fig. 2. *Phrygiopilus ibarrai* (Pretzmann, 1980), male from km 30 on road from José Pinula to Mataquesquintla, Guatemala Department, Guatemala (TU 6208): A–D, first left gonopod; A, caudal; B, apex, mesocaudal; C, apex, laterocephalic; D, apex, lateral; E, abdomen; F, dorsal view of right side of carapace; G, chela of largest cheliped, external view; H, third maxilliped; s, end of marginal process. Scale bars = 1 mm.

tercourses in Guatemala that drain into the Caribbean Sea (*Phrygiopilus chuacusensis* Smalley, 1970, *P. acanthophallus* Smalley, 1970, and *P. ibarrai*). *Phrygiopilus chuacusensis* is from a locality in karstic areas

drained by the Motagua river, while the other two species are from the headwaters of the Polochic river. The type locality of *P. strengeriae* (Pretzmann, 1965), stated to be “Trace Aguas, Caco”, Guatemala, could

not be located. According to Reddell (1981) the cave at Trece Aguas, Cacao, probably is in the karstic system Seamay-Sejul, where the holotype of *P. acanthophallus* was also collected (Smalley 1970). (2) Watercourses in the State of Chiapas, Mexico, flowing into the Gulf of Mexico (*Phrygiopilus yoshibensis* and *P. montebelloensis*). The first species is from the basin of the Grijalva river, the second from the Usumacinta river.

The six species of *Phrygiopilus* can be distinguished by characters of the first male gonopods, as follows.

- 1. Lateral lobe present; supra-apical process implanted on a sinuous peduncle *P. strengerae*
- Lateral lobe absent; supra-apical process sessile 2
- 2. Stout spines only on the supra-apical process 3
- Stout spines not confined to supra-apical process 5
- 3. Mesial process bifid *P. ibarraei*
- Mesial process conical 4
- 4. Supra-apical process rounded *P. acanthophallus*
- Supra-apical process subtriangular .. *P. chuacusensis*
- 5. Lateral process without stout spines; supra-apical process off main axis of gonopod, giving L-shaped appearance to apex *P. montebelloensis*
- Lateral process with stout spines; supra-apical process in line with main axis of gonopod *P. yoshibensis*

Genus *Ptychophallus* Smalley, 1964b

Ptychophallus osaensis, new species

Fig. 3

Material.—Costa Rica: Rincón de Osa, Puntarenas Province, 1971, 1 male holotype, cl. 28.5, cb. 47.9, 1 male paratype, cl. 19.9 mm, cb. 31.9 mm (TU 6271); Rincón de Osa, Puntarenas Province, Jul 1972, leg. R. Zeledón, 8 males, cl. 14.6–27.1 mm, cb. 22.6–43.7 mm, 1 mature female, cl. 32.4 mm, cb. 53.6 mm, 4 juvenile females, cl. 15.9–20.3 mm, cb. 24.5–32.4 mm (TU 6251).

Type locality.—Costa Rica: Rincón de Osa, Puntarenas Province.

Diagnosis.—First gonopods wide in caudal view, narrow in lateral view, strongly arched in caudo-cephalic direction, with lateral expansion divided into larger proximal rounded lobe, transversely directed toward caudal side, and distal knob-like lobe, transversely directed toward cephalic side and parallel to disto-caudal ridge in caudal view; disto-caudal ridge narrow, reaching level of median notch of lateral projection; apex of gonopods pedunculated, strongly bent toward latero-cephalic side, oval-oblong in distal view, lateral and mesial borders rounded and expanded, conspicuous notch on caudal border and semicircular thin ridge over spermatic channel; border of apical mesial process rounded, projected; mesial subapical process wide, rounded.

Description of holotype.—Carapace 1.70 times as wide as long, surface smooth, polished, except for scattered flat brown papillae over gastric and anterior branchial regions, near margins; cardiac and intestinal regions only faintly delimited by shallow, indistinct depressions; cervical grooves forming wide depression curving backwards, not reaching margins of carapace; anterolateral margins between external orbital angles and level of cervical grooves with shallow postorbital notch and faintly indicated papillae; rest of carapace margins with approximately 20 papilliform teeth, which are rounded at beginning of series and widely triangular posteriorly (Fig. 3F). Postfrontal lobes wide, transverse, delimited anteriorly by thin groove; median groove wide and deep, making V-shaped incision on upper margin of front. Surface of carapace between postfrontal lobes and front flat, slightly inclined forward and towards middle line. Upper margin of front in dorsal view slightly bilobed, divided into 2 halves by median notch, margin thin, well marked by small tubercles; lower margin of front thin, moderately sinuous, not conspicuously advanced in front of upper margin; both frontal margins subparallel.

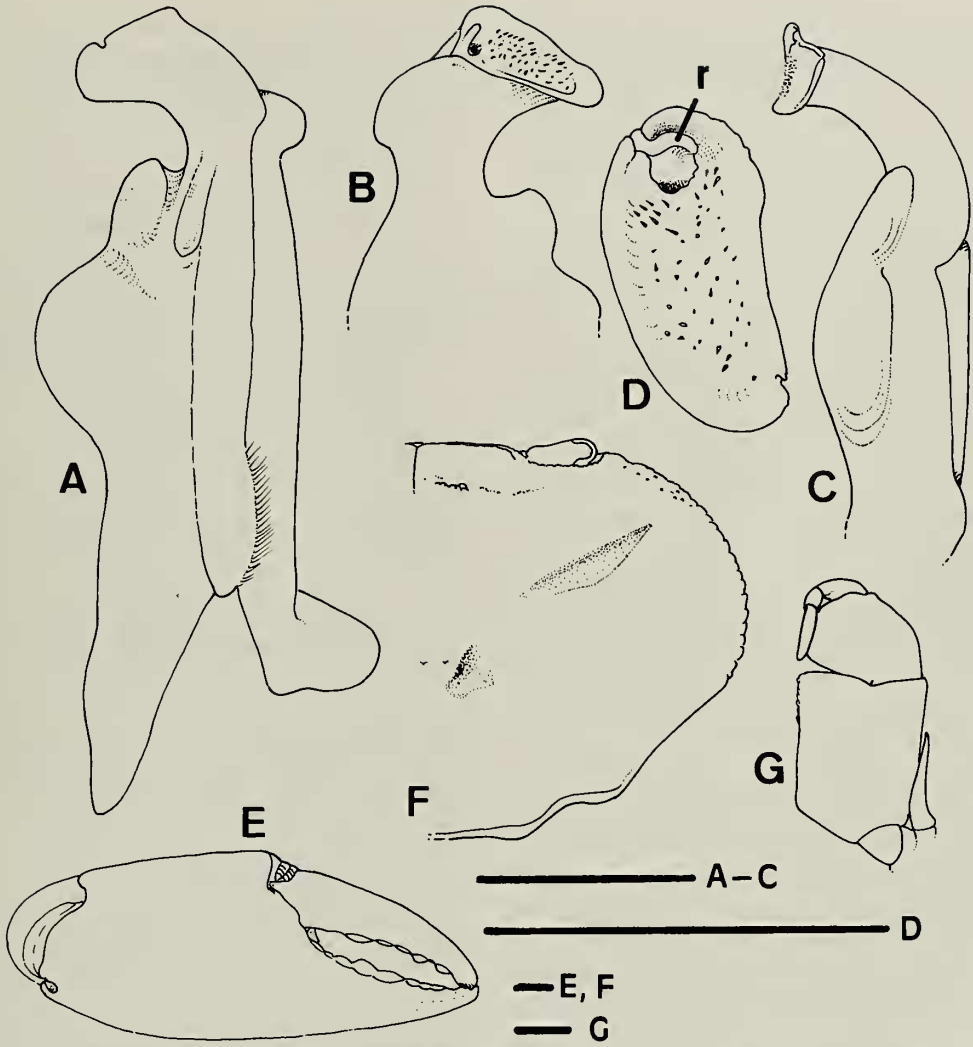


Fig. 3. *Ptychophallus osaensis*, new species, holotype male from Rincón de Osa, Puntarenas Department, Costa Rica (TU 6251): A-D, first right gonopod; A, caudal; B, apex, cephalic; C, apex, lateral; D, apex, distal; E, chela of largest cheliped, external view; F, dorsal view of right side of carapace; G, third maxilliped; r, ridge over spermatic channel. Scale bars = 2 mm.

Exognath of third maxilliped 0.66 length of ischium of endognath. Palm of largest cheliped (right) moderately swollen, upper margin convex, lower margin slightly sinuous, fingers gaping, rows of small black-brown points on external surface, teeth completely eroded (Fig. 3E).

First gonopods wide in caudal view, narrow in lateral view, strongly arched in caudo-cephalic direction. Lateral projection large (Fig. 3A), divided in 2 lobes by shallow

median notch; proximal lobe larger, rounded, transversely directed toward caudal side; distal lobe knob-like, transversely directed toward cephalic side, parallel to disto-caudal ridge in caudal view. Disto-caudal ridge narrow, reaching level of median notch of lateral projection (Fig. 3A). Subapical mesial process wide, rounded (Fig. 3B). Apex of gonopods pedunculated, strongly bent toward latero-cephalic side (Fig. 3C), applied against sternites when

abdomen closed; border of apical mesial process rounded, projected; profile of apex oval-oblong in distal view, lateral, mesial borders rounded and expanded, lacking conspicuous notch on caudal border; semi-circular thin ridge over spermatid channel (Fig. 3D, r) lacking flat papilla.

Etymology.—The species is named for the Osa Peninsula, Costa Rica, where the species was first collected.

Remarks.—*Ptychophallus osaensis* can be distinguished from all other species in the genus by the first gonopods which have a small knob-like lobe on the lateral expansion (Fig. 3A), a distinctly-shaped mesial subapical process (Fig. 3B) and a long geniculated apex (Fig. 3C). *Ptychophallus osaensis* and *P. tristani* (Rathbun, 1896) are the only species of this genus with a wide mesial subapical process of gonopods; in *P. osaensis* this process is regularly rounded, whereas in *P. tristani* the process is hatchet-shaped (Smalley 1964b).

Rodríguez & Hedström (2000) have shown that the first gonopods of *Ptychophallus* shows a progressive transformation of the apex, leading to the formation of an apical receptacle, possibly for the retention of spermatophora during copulation. The present new species belongs to the most primitive group of *Ptychophallus* (together with *P. colombianus* (Rathbun, 1893), *P. tristani* and *P. kuna* Campos & Lemaitre, 1999) characterized by a first gonopod with a wide lateral expansion and a pedunculated apex. This group also includes the male specimen recorded by Smalley (1964b) as *P. exilipes* (Rathbun, 1898). The type specimen of *P. exilipes* described by Rathbun was collected at El Coronel, on the Atlantic slope of Costa Rica, and is a female, so its status is uncertain. The specimen described by Smalley (1964b) from Costa Rica was collected at a locality on the Pacific slope, 50 miles south from the type locality, and most probably is not conspecific with Rathbun's (1898) species. The five species of *Ptychophallus* discussed here can be

distinguished from each other by characters of the first male gonopods, as follows.

1. Lateral expansion undivided 2
- Lateral expansion divided into two unequal segments 3
2. Mesial sub apical process digitiform *P. exilipes* (sensu Smalley 1964b)
- Mesial subapical process triangular *P. colombianus*
3. Proximal lobe of lateral expansion smaller than distal one. Mesial subapical process wide, hatchet-shaped *P. tristani*
- Proximal lobe of lateral expansion conspicuously larger than distal one 5
5. Mesial subapical process rounded *P. osaensis*
- Mesial subapical process flange like *P. kuna*

Raddaus Pretzmann, 1965

Raddaus bocourti (A. Milne Edwards, 1866)

Material.—Guatemala: Lago de Atitlán, 4 miles E of Panajachel, Solola Department, 6 Aug 1967, leg. A. E. Smalley & I. Smalley AES 313, 3 immature males, 13.6–18.7 mm, cb. 20.5–27.0 mm, 2 females cl. 13.0–33.1 mm, cb. 19.0–53.4 mm (TU 4461); Rio Piscaya, 2 km N junction National RT5–RT4, small tributary of Rio Piscaya, at 40 km N from Guatemala, Guatemala Department, 12 Aug 1967, leg. A. E. Smalley AES 408, 1 immature male, cl. 15.8, cb. 23.3 mm, 3 immature females, cl. 16.5–27.5 mm, cb. 25.0–44.0 mm (TU 5801); km 56 from Guatemala city on route 5 to Salamá, small tributary of Rio Grande, Department Guatemala, 16 Aug 1967, leg. A. E. Smalley AES 413, 2 immature males, 18.6 and 18.8 mm, cb. 27.7 and 29.8 mm (TU 5799); km 71 from Guatemala City, route 5 toward Salamá, small tributary of Rio Grande, Guatemala Department, 16 Aug 1967, leg. A. E. Smalley AES 412, 2 immature males, cl. 11.0 and 12.5 mm, cb. 16.2 mm and 18.0 mm, 3 juvenile females, cl. 8.0–10.8 mm, cb. 12.0–15.9 mm (TU 5802).

Belize: Dry Colombia River at Colombia

Forest Camp, Rio Grande drainage, 7 Jul 1971, leg. Greenfield, 1 male cl. 45.2, cb. 75.9 mm, 1 female with young under the abdomen, cl. 49.2 mm, cb. 81.2 mm (TU 6385).

Acknowledgements

I express my thanks to H. L. Bart, Jr., and J. F. Fitzpatrick, Jr. for the loan of this valuable collection, and to M. Taylor for his help with the handling of the material.

Literature Cited

- Alvarez, F., & J. L. Villalobos. 1998. Six new species of fresh-water crabs (Brachyura, Pseudothelphusidae) from Chiapas, Mexico.—*Journal of Crustacean Biology* 18:187–198.
- Bott, R. 1956. Dekapoden (Crustacea) aus El Salvador. 3. Süsswasserkrabben (*Pseudothelphusa*).—*Senckenbergiana Biologica* 36:229–242.
- Campos, M. R., & R. Lemaitre. 1999. Two new freshwater crabs of the genus *Ptychophallus* Smalley, 1964 (Crustacea: Decapoda: Brachyura: Pseudothelphusidae) from Panamá, with notes on the distribution of the genus.—*Proceedings of the Biological Society of Washington* 112: 553–561.
- Milne Edwards, A. 1866. Description de trois nouvelles espèces du genre *Boscia*, Crustacés Brachyures de la Tribu des Thelphusiens.—*Annales de la Société Entomologique de France* (4) 6: 203–205.
- Milne Edwards, H. 1853. Memoire sur la famille des Ocyropodien.—*Annales des Sciences Naturelles, Zoologie*, 3e série 20:163–228.
- Pretzmann, G. 1965. Vorläufiger Bericht über die Familie Pseudothelphusidae.—*Anzeiger der Mathematisch Naturwissenschaftliche Klasse der Österreichischen Akademie der Wissenschaften* (1) 1:1–10.
- . 1968. Neue Südamerikanische Süßwasserkrabben der Gattung *Pseudothelphusa*.—*Entomologisches Nachrichtenblatt, Wien* 15(1):1–15.
- . 1980. Von Dr. Ivo Poglayen-Neuwall 1975 in Mittelamerika gesammelte Krabben.—*Annalen des Naturhistorische Museum, Wien* 83:651–666.
- Rathbun, M. J. 1893. Descriptions of new species of American freshwater crabs.—*Proceedings of the United States National Museum* 16(959): 649–661.
- . 1896. Descriptions of two species of freshwater crabs from Costa Rica.—*Proceedings of the U. S. National Museum* 18(1071):377–379, pl. 29–30.
- . 1898. A contribution to a knowledge of the freshwater crabs of America. The Pseudothelphusinae.—*Proceedings of the United States National Museum* 21(1158):507–537.
- Reddell, J. R. 1981. A review of the cavernicole fauna of Mexico, Guatemala, and Belize.—*Bulletin of the Texas Memorial Museum* 27:1–327.
- Rodríguez, G. 1982. Les Crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae.—*Faune Tropicale* 22:1–223.
- , & J. F. Fitzpatrick Jr. 1996. Alfred Evans Smalley.—*Journal of Crustacean Biology* 16: 214–215.
- , & R. von Sternberg. 1998. A revision of the freshwater crabs of the family Pseudothelphusidae (Decapoda: Brachyura) from Ecuador.—*Proceedings of the Biological Society of Washington* 111:110–139.
- , & I. Hedström. 2000. The freshwater crabs of the Barbilla National Park, Costa Rica (Crustacea: Brachyura: Pseudothelphusidae), with notes on the evolution of structures for spermatophore retention.—*Proceedings of the Biological Society of Washington* 113:120–125.
- Saussure, H. de. 1857. Diagnoses de quelques Crustacés nouveaux de Antilles et de Maxique.—*Revue et Magasin de Zoologie Pure et Appliquée* (2) 9:304–306.
- Schmitt, W. L. 1969. Colombian freshwater crabs notes.—*Proceedings of the Biological Society of Washington* 82:93–112.
- Smalley, A. E. 1964a. A terminology for the gonopods of the American river crabs.—*Systematic Zoology* 13:28–31.
- . 1964b. The river crabs of Costa Rica, and the subfamilies of the Pseudothelphusidae.—*Tulane Studies in Zoology* 12:5–13.
- . 1965. Two new freshwater crabs from Nicaragua.—*Annals and Magazine of Natural History* (13) 7 (83) 1964 (1965):651–656.
- . 1970. A new genus of freshwater crabs from Guatemala, with a key to the Middle American genera (Crustacea, Decapoda, Pseudothelphusidae).—*American Midland Naturalist* 83:96–106.